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NOTES ON THE PALEOCENE LAGOMORPH, *EURYMYLUS*[1]

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In 1925, Matthew and Granger described two forms from the Paleocene Gashato formation of Mongolia as *Eurymylus* and *Baënomys*. The upper teeth, described as *Eurymylus*, were referred to the Menotyphla. Although no specific decision was made as to the relationships of *Baënomys*, comparisons were made with simplicidentate rodents and with lagomorphs. These authors state (1925, p. 6) that "The pattern of the molars suggests the more hypsodont genera of pocket-mice, but has more definite suggestion of the Lagomorpha." The specimen originally described as *Baënomys* is a mandible, and that described as *Eurymylus* is a maxilla. In 1929, Matthew, Granger and Simpson described additional specimens, reached the conclusion that these remains were all referable to the same form, and selected *Eurymylus* as the valid genus, since it was represented by better material. They state (1929, p. 7) that "The zygomatic arch is not like that of known rodents, but the evidence does not more strongly favor any other allocation. . . .In both upper and lower teeth there is a superficial resemblance to the lagomorphs, but in some characters it is more specialized than even the recent Lagomorpha, and these specializations are in a direction so unlike any known member of the group that it is probable that *Eurymylus* does not belong in the duplicidentate division of the Order. To the non-lagomorph characters of the lower jaw previously mentioned (Matthew and Granger, 1925, p. 6) may be added the fact that the incisor in *Eurymylus* extends far back beneath the cheek teeth. The upper teeth are indeed transverse, but otherwise they show little evidence of lagomorph specializations and even aside from the absence of P^2, more definitely resemble primitive simplicidentates."

Some years ago, I reached the conclusion that there was no justifiable basis for comparing these Mongolian forms with the heteromyids or geomyids, all resemblances being rather superficial parallelisms between *Eurymylus* and the most specialized members of the two rodent families. Detailed comparisons were recently made between the lagomorphs and *Eurymylus* in connection with my paper on the White River lagomorphs (Wood, 1940). In the course of these studies, numerous similarities between the Oligocene lagomorphs and *Eurymylus* were noted, and the conclusion was tentatively reached that the latter form is a lagomorph (Wood, 1940, p. 358). The present paper is an effort to present the data on which this conclusion was based, and to show that recent additions to our knowledge of the earlier lagomorphs, particularly as to their tooth pattern, show that Matthew, Granger and Simpson's objections to this relationship do not appear to be as strong as they did ten or fifteen years ago.

This review is based on all the known specimens of this genus, all of which are in the American Museum. These are A. M. N. H. Nos. 20422, 20424, 21735, 21737 and 21738. All of these specimens are very fragmentary, consisting only of broken lower jaws, showing all or part of the cheek tooth series, together with maxillary dentitions. One specimen, A. M. N. H. No. 21737, is worthy of more detailed study than it has previously been given, since, in addition to the left upper cheek teeth, it retains parts of the palate and part of the zygoma and face.

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I wish to express my appreciation to The American Museum of Natural History, and particularly to Drs. Walter Granger and G. G. Simpson, for permission to study this material and for the publication of this report. Figure 1 was drawn by Mr. John Germann, and the other figures by the author. This study was assisted by a grant from the Marsh Fund of the National Academy of Sciences.

The shape of the zygoma is superficially different from that in leporids and ochotonids, but the muscular attachments appear to have been in fundamentally the same positions as in the later forms. The anterior face of the zygoma slopes backward at a sharp angle below the orbit, instead of being almost vertical as it is in the rabbits, but this is a more primitive condition through which the leporids must have passed, and is entirely expectable in a more primitive group of animals that presumably had a lesser development of propalinal mastication and, associated therewith, a smaller masseter, presumably acting more nearly vertically. The free portion of the zygoma begins beside M^1, and the anterior end of the masseteric fossa is by the middle of P^4. In neither of these features does *Eurymylus* differ appreciably from *Palaeolagus*. The masseteric fossa of *Eurymylus* is confined to the maxillary. There appears probably to have been a postorbital process of the maxillary, and certainly to have been a pit on the lateral face of the maxillary above the masseteric fossa, both as in leporids. There is absolutely no similarity in the zygomatic region between *Eurymylus* and *Caenotherium* (which has sometimes been suggested as showing lagomorph similarities) or between *Eurymylus* and any rodent with which I have compared it.

The infraorbital foramen is large, as in *Palaeolagus*, and rather similarly placed. It is, however, anterior to the tooth series, rather than above P^2 as in *Palaeolagus*. In part at least, this difference is referable to the absence of this tooth in *Eurymylus*. There is an extensive pitting of the maxilla, which appears to be an incipient stage of the fenestration so characteristic of the lagomorphs, and which I do not recall having seen in just such a form in any other group. In *Eurymylus*, this pitting is confined to the space between the infraorbital foramen and the zygoma (Fig. 1), rather than being above the foramen as in *Palaeolagus*. Whatever the cause of the extensive maxillary fenestration in the lagomorphs, the pitting in *Eurymylus* appears to represent an ideal initial stage through which the lagomorphs must have passed, although the difference in the area in which the pitting is taking place suggests that *Eurymylus* is not on the direct line of ancestry to the Eocene and later lagomorphs.

The malar is a thin vertical plate of bone, rather similar to that in the rabbits, and appears to lie along the inner side of the maxillary almost to the front of the orbit.

The palate is broken at both ends, but the posterior end of the anterior palatine fenestra is clearly visible. It is separated from the mid-line by a rather thick septum of bone. The posterior end of the fenestra is immediately in front of P^3, approximately in the same position as in various genera of leporids (Wood, 1940, pp. 283–284). The posterior part of the palate is so cracked that nothing can be said of the position of the maxillary-palatine suture, of the posterior nares, or of the posterior palatine foramina. There is no indication that the palate was not essentially as narrow as in the early rabbits, and of uniform width between the tooth rows, a lagomorph character.

One of the two specimens showing the upper teeth, A. M. N. H. No. 21737, is so broken that it cannot certainly be determined whether or not P^2 was present. However, in the other specimen showing the upper dentition (A. M. N. H. No. 20422), it is apparent that this tooth was absent. If this tooth had originally been present in A. M. N. H. No. 21737, it must have been as small and non-functional as is P^3 in modern sciurids. Although it is possible that P^2 was present in some specimens, it seems very much more likely that the dental formula of *Eurymylus* was $P\frac{2}{2}$, $M\frac{3}{3}$. It by no means follows, of course,

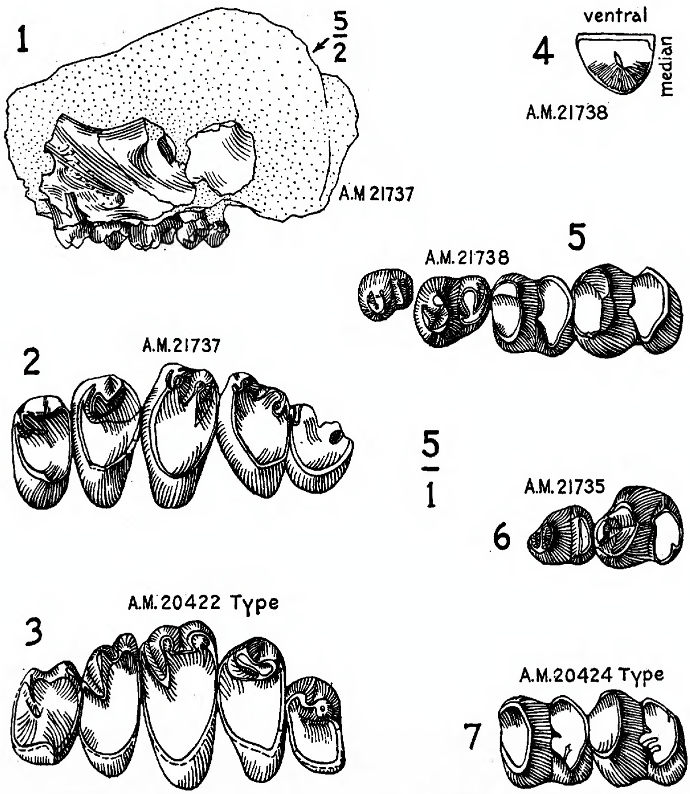

Fig. 1. Lateral view of left side of maxilla and zygoma, *Eurymylus laticeps*, A. M. N. H. No. 21737, $\times 2^1/_2$.
Fig. 2. P^3–M^3 left, *Eurymylus laticeps*, A. M. N. H. No. 21737, $\times 5$. Anterior end to the left.
Fig. 3. P^3–M^3 right, type of *Eurymylus laticeps*, A. M. N. H. No. 20422, $\times 5$. Anterior end to the right.
Fig. 4. Cross section of left lower incisor, *Eurymylus laticeps*, A. M. N. H. No. 21738, $\times 5$. Ventral side to the top, median side to the right.
Fig. 5. P_3–M_2 left, *Eurymylus laticeps*, A. M. N. H. No. 21738, $\times 5$.
Fig. 6. P_3–P_4 right, *Eurymylus laticeps*, A. M. N. H. No. 21735, $\times 5$.
Fig. 7. M_1–M_2 left, *Eurymylus laticeps*, A. M. N. H. No. 20424, $\times 5$. (Type of *Baënomys ambiguus*.)

that contemporary relatives of *Eurymylus* may not have retained this tooth. It should also be pointed out that, in the earliest known leporids, P^2 is a very small and apparently degenerate tooth, which subsequently becomes of more importance.

As Matthew, Granger and Simpson pointed out (1929, p. 5), the lower teeth of *Eurymylus* are already hypsodont, though still rooted. The upper teeth, as in the Oligocene leporids, are not as far advanced in this respect as are the lowers, but there is already a bilateral dissimilarity in height of crown, which would be the first step toward the unilateral hypsodonty seen in earlier leporids, especially in *Desmatolagus*.

In the lower teeth, the talonid of one tooth is at the same level as the trigonid of the one behind it, in exact agreement with the condition in the lagomorphs (Wood, 1940, p. 304), so that the two together form a flat surface, sloping upward to the rear, occluding with the flat surface of an entire upper tooth, which likewise slopes upward to the rear. To remove all doubt of the correct association of *Baënomys* and *Eurymylus*, experiments were made to determine how well the teeth of the two forms would occlude. Only two specimens (Nos. 20424 and 21737) are from the same side

and in about the same stage of wear. These two specimens occlude as well as could be expected of specimens representing different individuals of the same species.

Although the only available upper teeth of *Eurymylus* are very badly worn (Figs. 2–3), they show numerous features that are very reminiscent of the upper teeth of Oligocene leporids (Wood, 1940, Figs. 71, 81, 106 and 111). In all the upper teeth of *Eurymylus*, there is a small buccal section, consisting of two cusps, supported by two roots. These two cusps are bounded anteriorly and posteriorly by an elevated cingulum. In P^3, this cingulum does not quite reach the buccal margin of the tooth. The anterior cingulum of the premolars and the posterior cingulum in the molars remain independent longer than any of the other external portions of the tooth. The valley between this free element and the rest of the buccal part of the crown extends well into the central part of the crown. There is some evidence that these valleys originally extended well into the central part of the tooth, as in *Desmatolagus* (compare Fig. 3 and Wood, 1940, Fig. 111). The lingual two-thirds of the crown is becoming unilaterally hypsodont, and is supported by an enlarged lingual root. Upon wear, this portion of the tooth becomes a broad basin of dentine, with no trace of an enamel pattern. In some teeth, apparently less worn than others, there is a slight trace of a lingual fold, which appears to be homologous to the lingual fold in leporid teeth, and to have originally separated two lingual elements of the crown from each other. All of the above-described features agree almost exactly with the conditions in *Palaeolagus*, *Megalagus* and *Desmatolagus*, and are much less like any other forms with which I have compared *Eurymylus*.

There are three mental foramina, one just below P_3, one slightly in front of it, and the third below P_4. This is similar to the situation in *Palaeolagus*, where two foramina are present, one below P_4 and one in front of P_3. The alveolar border of the diastema is pinched up into a sharp ridge, a feature that is characteristic of all the Leporidae. The masseteric fossa is low on the mandible, forming a slight knob beneath the anterior end of M_3, also as in *Palaeolagus*, but resembling other leporids, though to a lesser degree. What little can be seen of the masseteric fossa is very suggestive of the leporids. The lower incisor extends at least as far posterad as beneath M_2, and probably farther, differing in this from the Eocene and later lagomorphs. However, as previously pointed out, among the known leporids "there has been a very marked proportionate reduction in the length of the lower incisor since White River time, and . . . perhaps a slight reduction between Uinta and White River. The most obvious explanation of this reduction is that the growth of the prisms of the lower cheek teeth interfered with the functioning of the enamel organ of the lower incisor, and that, following the path of least resistance, the latter migrated forward." (Wood, 1940, p. 298.)[1] In view of this proportional reduction since the Uintan, there is no reason to consider that a similar reduction may not have been taking place since the Paleocene as well. The incisor has a flat anterior face, with the enamel limited to the flat surface, and with radiating dentine tubules (Fig. 4). This flat anterior face is similar to that in *Palaeolagus* and later leporids, but is a difference from *Mytonolagus*. It appears that the symphysis extends nearly as far back as P_3, and the position and curvature of the incisor indicate that it would erupt not far from the front end of this tooth, suggesting a rather short diastema for a lagomorph, which is probably a primitive character.

Two specimens show the premolars not fully erupted (A. M. N. H. Nos. 21735 and 21738). In both of these, P_3 is less worn than P_4, so that it seems certain that this is a normal development. This is in exact agreement with the conditions in *Palaeolagus* (Dice and Dice, 1935, p. 461). In P_4, the enamel is very thin on the anterior and posterior sides of the

[1] This statement, of course, is not intended to be a causal explanation of the conditions, but merely a descriptive summary of what appears to have taken place.

talonid, and thicker on the lateral sides, which appears to foreshadow the reduction and elimination of the enamel that occurs in these portions of the teeth in the Oligocene and later lagomorphs.

Both P_3 and P_4 have a pattern clearly derivable from a tuberculosectorial ancestry, with cusps that can easily be identified as paraconid, metaconid and protoconid, connected by crests to form a V-shaped trigonid, and the hypoconid and entoconid, together with an elevated posterior cingulum, forming a V-shaped talonid. This is much morec learly shown in A. M. N. H. No. 21738 than in the slightly more worn A. M. N. H. No. 21735 (Figs. 5–6). Perhaps the published figure of a lagomorph best suited for comparison is that of *Palaeolagus temnodon*, given by Wood (1940, Fig. 84). This shows a trigonid on P_3 that is essentially identical with that of *Eurymylus* except for the reduction of the paraconid in the Oligocene form, a reduction which is apparently already taking place in the Mongolian genus (see Fig. 6). The talonid of P_3 is much simpler in *Eurymylus* than in *Palaeolagus*, but the parts all appear to be similar. One notable difference between these teeth in the two genera is that in *Palaeolagus* the talonid of P_3 is wider than the trigonid, whereas in *Eurymylus* the reverse is the case.

The lower molars clearly show another lagomorph feature in the reduction or absence of the enamel on the anterior faces of both trigonid and talonid (Figs. 5 and 7). This is a feature that does not prove relationship, but is definitely suggestive of it. The remnants of the pattern in the molars of one specimen (Fig. 7) are very suggestive of a pattern resembling that of *Palaeolagus* (Wood, 1940, Figs. 76 and 85). I have met this type of pattern nowhere except in *Eurymylus* and the lagomorphs.

The tooth measurements of all the known specimens of *Eurymylus* are given in the accompanying table. Matthew, Granger and Simpson remarked that "In No. 21738, P_4 is smaller than in No. 21735, and they may prove to represent distinct species" (1929, p. 6). This distinction is clearly brought out by the table of measurements, as is also the difference in size between No. 21738 and No. 20424. These differences in size, however, appear to me to be merely differences due to the amount of eruption from the alveoli, and to be an early step in the process previously pointed out in the lagomorphs (Wood, 1940, p. 318), where growth of the tooth makes it difficult, if not impossible, to measure homologous parts of the teeth in individuals of different ages. As all the lower jaws of *Eurymylus* represent individuals of slightly different ages, I should expect, if this animal actually was a lagomorph, that the tooth measurements would vary to a considerable degree with age. The upper teeth of the two known specimens are more nearly the same age, and the tooth measurements are more nearly uniform, as would be expected. The greatest differences in measurement here are in the transverse diameters, which once again is expectable in lagomorphs.

The following table has been prepared to summarize the resemblances and differences between the later Tertiary lagomorphs on the one hand and *Eurymylus* on the other.

COMPARISON OF *Eurymylus* AND LAGOMORPHS

Similarities

Fenestration of maxilla, incipient in *Eurymylus* as pitting
Position of the anterior root of the zygoma
Position and size of the infraorbital foramen
Shape and position of malar
Position of anterior palatine fenestra
Shape of palate
Unilateral hypsodonty of upper cheek teeth
Method of occlusion of cheek teeth
Orientation of lower cheek teeth so that talonid of one tooth and trigonid of next succeeding tooth form a level surface
Large lingual basin in the upper teeth and the small buccal cusps, which do not receive much wear
There is perhaps a post orbital process on the maxilla of *Eurymylus*
Pit on lateral face of maxilla above masseteric fossa
Several mental foramina
Shape of masseteric fossa of mandible

Dissimilarities

Absence of P^2 in *Eurymylus*
Length of lower incisor, which extends posterad of M_2 in *Eurymylus*

Measurements of Teeth of *Eurymylus*

(All measurements in millimeters)

		A. M. N. H. No. 21737	A. M. N. H. No. 21738	A. M. N. H. No. 21735	A. M. N. H. No. 20422 *E. laticeps*, type	A. M. N. H. No. 20424 *Baënomys ambiguus*, type
P^3	anteroposterior	1.49	—	—	1.33	—
	width protoloph	2.48	—	—	2.22	—
	width metaloph	2.58	—	—	2.12	—
P^4	anteroposterior	1.75	—	—	1.73	—
	width protoloph	3.16	—	—	3.60	—
	width metaloph	3.31	—	—	3.25	—
M^1	anteroposterior	1.95	—	—	1.92	—
	width protoloph	4.00	—	—	4.15	—
	width metaloph	3.78	—	—	3.95	—
M^2	anteroposterior	1.80	—	—	1.49	—
	width protoloph	3.08	—	—	3.63	—
	width metaloph	2.67	—	—	3.25	—
M^3	anteroposterior	1.58	—	—	1.67	—
	width protoloph	2.13	—	—	2.50	—
	width metaloph	1.87	—	—	2.18	—
P_3	anteroposterior	—	±1.35	1.68	—	—
	width trigonid	—	±1.00	1.19	—	—
	width talonid	—	±0.90	1.23	—	—
P_4	anteroposterior	—	1.97	2.22	—	—
	width trigonid	—	1.71	1.93	—	—
	width talonid	—	1.22	1.63	—	—
M_1	anteroposterior	—	2.09	—	—	2.20
	width trigonid	—	1.92	—	—	2.23
	width talonid	—	2.05	—	—	2.24
M_2	anteroposterior	—	2.40	—	—	2.34
	width trigonid	—	2.18	—	—	2.42
	width talonid	—	2.08	—	—	2.04
M_3	anteroposterior	—	—	—	—	—
	width trigonid	—	—	—	—	—
	width talonid	—	—	—	—	—

Anterior face of the zygoma slopes in *Eurymylus* rather than being vertical as in lagomorphs

Pitting below infraorbital foramen rather than above

It is believed that none of the features listed in the second section of the foregoing table are indicative of a wide divergence between *Eurymylus* and the lagomorphs. The length of the lower incisor and the absence of P^2 in the Paleocene form may show that *Eurymylus* is not on the direct line of ancestry to the later lagomorphs, or merely that there has been a reversal of evolution in the interval from the Paleocene to the Uintan, which is entirely within the realms of possibility. I am inclined to believe that the first explanation holds for the absence of the premolar, and the second for the condition of the incisor.

The similarities listed above show, I believe, that *Eurymylus* must definitely be included among the lagomorphs. Although the fenestration of the maxilla is not in the same position in *Eurymylus* and *Palaeolagus*, the general appearance of the fenestrations is exceedingly similar, and it seems entirely reasonable to assume that these similarities result from identical mutations of homologous genes.

Although *Eurymylus* thus appears to belong among the Lagomorpha, it cannot be placed in either the Leporidae or the Ochotonidae. Matthew, Granger and Simpson (1929, p. 5) erected a new family, Eurymylidae, defined as follows: "Cheek teeth P^2_2 M^3_3. Lower incisor fully gliriform, extending far back beneath cheek teeth. Lower cheek series hypsodont, rooted, with elevated trigonids and low talonids, each wearing to a transverse enamel ring. Upper cheek teeth strongly

transverse, tritubercular, with a tendency to form anterior and posterior molar cingula. Masseter origin confined to zygoma, insertion not extending forward of posterior end of M_3. Infraorbital foramen small." In addition to these features, I would add that the upper cheek teeth are beginning to develop unilateral hypsodonty of a typical lagomorph type, and that there is incipient fenestration of the maxilla. I believe that the Eurymylidae represent an ancestral stock from which the Leporidae and Ochotonidae have been derived. For the time being, and in view of how little is known of lagomorph evolution, all that can be done is to group the three families in the order, placing the Eurymylidae in a generally ancestral position. It seems probable that, when more care shall have been taken in the study of the Leporidae and Ochotonidae, it may prove necessary to raise these families to superfamilies, but there is no justification for taking such a step at the present time.

In summary, it would appear that *Eurymylus* is the type and only known genus of the family Eurymylidae which represents a very early group of lagomorphs. Although *Eurymylus* is unquestionably not ancestral to the Eocene and later lagomorphs, there is no known reason why a near relative could not fill such a position, since the only character listed in the family definition that would rule this genus out of the line of lagomorph evolution is the absence of P^2, which could very well have been retained by a related genus. Moreover, there is no reason why the tooth could not have been lost and subsequently regained, as appears to happen sometimes in dogs (Wood and Wood, 1933). Such an evolutionary background might explain why P^2 of *Palaeolagus* is so unusual in its cusp arrangement.

If *Eurymylus*, as here postulated, is actually a lagomorph, it carries the ancestry of this group back to the upper Paleocene, and shows them still widely diverse from all their known contemporaries. Unfortunately, although it is possible to find many lagomorph characters in the teeth of *Eurymylus*, it is still not possible clearly to evaluate the upper teeth of this genus in tritubercular nomenclature. The lower teeth appear to be definitely tuberculosectorial, but an analysis of the upper ones will have to await better material.

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